



Past and future impact of climate change on foraging habitat suitability in a high-alpine bird species: Management options to buffer against global warming effects

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ABSTRACT

The majority of predictions about the impacts of climate change on wildlife have relied either on the study of species' physiological tolerance or on broad-scale distribution models. In comparison, little attention has been paid to species' mechanistic responses to fine-grained, climate-induced modifications of habitat suitability. However, such studies would be pivotal to the understanding of species' ecological requirements (and hence their adaptive potential to environmental change) and the design of management strategies. We investigated foraging microhabitat selection in a potentially climate-change sensitive species, the white-winged snowfinch *Montifringilla nivalis*, during the breeding season in the Alps. Our microhabitat selection model considered topography, ground-cover variables and sward height within a 5-m radius at foraging and control locations. Habitat selection was positively affected by grassland cover, negatively by sward height and quadratically by snow cover (optimum around 40%); birds avoided anthropized (urban areas, roads) sites. We estimated past (1976) and future (2066) climate-driven changes in foraging microhabitat suitability, assuming a progressively earlier date of snowmelt due to increasing temperatures over this entire time span. We then modelled the potential impact of snowmelt (and related sward height) on habitat suitability under two scenarios: maintaining the current situation (i.e. irregular seasonal grazing) and implementing targeted management in an attempt to mitigate impacts of earlier snowmelt. Predicted foraging habitat suitability (estimated as the fraction of suitable plots) significantly declined over time (–23% between 1976 and 2016, further 32% loss by 2066). However, model outputs demonstrated that maintaining sward height below 6 cm on breeding grounds (e.g. by regular grazing) would significantly decrease the predicted loss of suitable foraging habitat. Detailed information about patterns of resource exploitation allows the identification of mechanistic, functional responses of species to environmental change, and enables an evaluation of habitat management options that can buffer against the detrimental effects of global warming.

1. Introduction

Anthropogenic climate change is increasingly threatening ecosystems and species worldwide (IPCC, 2013; Rosenzweig et al., 2008).

Evidence from a wide range of taxa and ecological systems suggests that climate change has already started to affect biodiversity at a global scale (e.g. Carnaval and Moritz, 2008), for instance by modifying species distributions, altering their habitats or increasing extinction risk

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due to rapid shifts in abiotic conditions (Chen et al., 2011; Parmesan and Yohe, 2003). Based on forecast climatic scenarios, several studies have furthermore attempted to predict future climatic impacts on biodiversity (e.g. Bellard et al., 2012; Thomas et al., 2004).

The potential effects of climate, and hence of climate change, on animal species have been mostly assessed either by experimental approaches evaluating physiological tolerance to climate variations (e.g. temperature) at the individual level (Johnson, 1968) and under controlled environments (Chapin et al., 1995), or via large-scale distribution models, the latter representing one of the commonest ways to explore potential changes in species distributions owing to climate change (Fitzpatrick and Hargrove, 2009; Hijmans and Graham, 2006). Eco-physiological investigations usually include field observations and laboratory measurements that aim to detect how alterations of environmental constraints influence species' physiological responses and hence population processes (Arlettaz et al., 2000; Pörtner and Knust, 2007). In contrast, correlative models of species distribution (Guisan and Thuiller, 2005) rely on environmental factors such as climate, land-cover and topographic variables, which are usually linked with species occurrence at a broad scale, and thus can help to identify those species that are most likely to be affected by climate or environmental change in a given area. They can, to some extent, be downscaled to the territory/home-range size of a target species (Brambilla et al., 2015; Braunisch et al., 2013), but often remain fairly limited in their predictive power as they may miss essential mechanistic components (Williams and Jackson, 2007) linked to patterns of resource exploitation, such as food acquisition. Hence, species distribution models may not embrace species' niche complexity as a whole (Braunisch et al., 2013) and may both over- and underestimate extinction risk due to climate change (Bellard et al., 2012). Although species distribution models are indeed the most widely used (and scalable) approach to assess species' spatio-temporal responses to climate change (Engler et al., 2017; Moritz and Agudo, 2013), there is a need for complementary approaches that integrate finer-scale ecological information for, on the one hand, improving our mechanistic understanding of the tolerance and resilience, i.e. the adaptive potential of target organisms to shifting environmental conditions (e.g. Baudier et al., 2015; Bennett et al., 2015), and, on the other hand, modelling appropriately the consequences of environmental changes upon population dynamics (Fedy and Martin, 2011; Fordham et al., 2017). This could be addressed by considering the impacts of climate change upon fine-scale habitat structure and availability (henceforth, microhabitat), which eventually drives habitat suitability. However, this aspect has received comparatively little attention so far, despite its crucial importance in understanding mechanistic responses of species to environmental change (Fordham et al., 2017; Kearney and Porter, 2009). Fine-grained species-habitat associations are essential to understand how changes in microhabitat due to climate change will affect species' habitat suitability at local and broader scales, which will ultimately influence a species' ability to respond to climate-induced environmental changes (Scheffers et al., 2014).

Studies of the effects of microhabitat alteration due to changing climatic conditions have mostly focused on small-sized organisms (e.g. invertebrates) that are highly sensitive to local climatic/habitat variation, especially due to their strong temperature-dependent life-cycles (Davies et al., 2006). Pincebourde et al. (2016) have shown that microhabitat properties shape species responses to climate change. Research has generally focused on species with limited mobility (e.g. plants (Pradervand et al., 2014), benthic invertebrates (Schiel et al., 2004)). In contrast, studies on the distribution of terrestrial and highly-mobile species usually deal with broad spatial scales, despite the fact that habitat selection in these species operates at multiple scales. In birds for instance, this concerns the selection of breeding sites (Jedlikowski et al., 2016; Rauter et al., 2002), foraging grounds (Brambilla et al., 2017b; Martínez-Miranzo et al., 2016; Schaub et al., 2010), and even shelters to avoid unsuitable climate (Visinoni et al.,

2015). An absence of information about microhabitat preferences can lead to serious biases in predictions of climate change effects on species' distributions (cf. Bellard et al., 2012). As a matter of fact, microhabitat characteristics may allow species persistence when the general climate of the region appears to have become unsuitable, and vice versa. Studies of microhabitat suitability are thus pivotal to our basic understanding of species' ecological requirements and to devise efficient conservation management of climate-sensitive biodiversity. Several such studies have emerged recently (Suggitt et al., 2011; Turlure et al., 2010), which have established the importance of both microhabitat and microclimate to understand the sensitivity of species to environmental shifts and, ultimately, their population dynamics and distribution patterns (Fedy and Martin, 2011; Frey et al., 2016). The basic question here can thus be formulated as follows: to which extent can microhabitat characteristics, and their potential management, buffer against any detrimental effects of overall climate change (e.g. Braunisch et al., 2014)?

Among terrestrial organisms, high-elevation cold-adapted species seem to be particularly vulnerable to climate change (Dirnböck et al., 2011; Lagerholm et al., 2017; Scridel et al., 2018), with their future distribution being either expected to contract towards higher elevations due to ambient temperature warming (Braunisch et al., 2013; Chamberlain et al., 2013; La Sorte and Jetz, 2010; Pernellet et al., 2015; Sekercioglu et al., 2008), or to vary in a complex way in response to shifts in precipitation regimes that remain difficult to forecast (e.g. Tingley et al., 2012). Mountain areas are indeed subject to higher rates of warming compared to the global average (e.g. Böhm et al., 2001; Brunetti et al., 2009), yet at the same time, they are also experiencing strong changes in landscape and land use (e.g. forest encroachment in abandoned pastures, upward treeline shift or loss of areas permanently covered by snow). High-elevation ecosystems thus represent an ideal setting to investigate the fine-grained impact of environmental change on habitat and biocenoses, especially due to the complex topography, including steep elevational gradients, that generates a large range of microhabitats and microclimates (hereafter topoclimates) and offers numerous refugia opportunities (Körner and Ohsawa, 2006). Such heterogeneity may per se represent a chance to maintain biodiversity, either naturally (Brambilla et al., 2016) or through informed conservation management (Braunisch et al., 2014). However, to the best of our knowledge, mitigation strategies to maintain niche opportunities for high-alpine biodiversity facing climatic risks have not been investigated so far (Shoo et al., 2011; Turlure et al., 2010).

In this study, we investigated the foraging microhabitat selection in a high-elevation, cold-adapted and snow-exploiting passerine bird, the white-winged snowfinch *Montifringilla nivalis* (Aves: Passeridae; henceforth: snowfinch), during the nestling rearing period, a crucial phase of the life-cycle. The snowfinch is a mountain specialist species breeding at high elevations above the treeline (in the European Alps mostly between 1800 and 3000 m asl; Cramp and Perrins, 1994). Nests are usually located in rock crevices or human-built infrastructure such as mountain buildings or ski-lift pylons (Cramp and Perrins, 1994). Females lay the first clutches of 4–5 eggs during the second half of May to early June, and nestlings fledge at ca.18–22 days of age (del Hoyo et al., 2009). During the nestling rearing period, adults collect invertebrate prey in the surroundings of nest sites, usually within 300 m of the nest, frequently on or at the margin of melting snow patches and in alpine grasslands (Antor, 1995; Brambilla et al., 2017b; Catzeffis, 1975; Cramp and Perrins, 1994; Strinella et al., 2007).

A recent study of foraging habitat selection by breeding snowfinches in the Italian Alps highlighted the importance of habitat factors that are largely climate-dependent, such as snow cover (positively selected), height of the grass sward (lower sward preferred), and solar radiation (lower values favoured, especially late in the season, indicating avoidance of warmer sites). This previous study was based on 314 m² plots (i.e. at a meso-scale) and did not explicitly address the key question of climate change effects on habitat suitability (Brambilla

et al., 2017b). Based on the outcome of correlative distribution models which accounted for climatic, topographic and land-cover variables, both at the landscape (Maggini et al., 2014) and the territory level (Brambilla et al., 2016), the snowfinch is expected to undergo a marked range contraction in the Alps because of climate change, especially due to increases in ambient temperature and habitat loss, snow cover being a key component in the species' ecology (Brambilla et al., 2017b). In this study, we focus on assessing the magnitude of climate change effects on the suitability of foraging habitats, and identifying habitat management measures at the territory-level scale that might help mitigate some detrimental effects of climate change. More specifically, our aims were: 1) to identify key habitat factors driving foraging microhabitat selection during food provisioning to nestlings by parents in a wide area of the Central Alps; 2) to evaluate past and forecast future changes in foraging microhabitat suitability by building models of microhabitat suitability, based on longitudinal data (both historical and projected) on changing snowmelt date, which has become progressively earlier in recent decades (by c. 6 days per decade; Klein et al., 2016); and, 3) to assess whether habitat management operations could maintain microhabitat suitability in the face of climate change. To the best of our knowledge, this is the first study to explicitly model the potential impact of climate change on foraging microhabitat suitability in a terrestrial vertebrate. Our study paves the way for better forecasts of wildlife responses to climate-induced alterations of habitat, and provides targeted conservation guidance for maintaining suitable foraging grounds in the face of climate change.

2. Methods

2.1. Study area and data collection

We investigated foraging microhabitat selection by 22 snowfinch breeding pairs from 8 different study sites (Sorebois, Zermatt, Furka Pass, Valle Spluga, Stelvio, Gavia, Passo Sella, Rosetta) of the Swiss and Italian Alps (Fig. 1). The elevation of the study sites ranged from 1880 to 2840 m a.s.l., adequately covering the elevational and macroclimatic gradient of snowfinch distribution in the Alps. All surveys were carried out between 14th June and 26th July 2016, focusing exclusively on snowfinches collecting food for nestlings (nestling-rearing period). First, by means of direct observations, we located snowfinch breeding pairs and active nests. Once an occupied nest was located, we adopted the following field protocols in order to record foraging and random points (hereafter, foraging and control plots).

In Switzerland, we mist-netted at least one parent from each monitored breeding pair to attach a radio-transmitter (Holohil Systems Ltd., model BD-2, weight: 1.4 g – corresponding to 3.2–3.9% of our birds' body mass, life span: 9 weeks) to its back using a leg-loop harness (Naef-Daenzer et al., 2001; Rappole and Tipton, 1991). As soon as tagged birds were provisioning food to the nestlings, foraging events were monitored over 2–6 days (spread along the nestling rearing period) with the aid of a hand-held three-element foldable Yagi antenna wired to a radio-receiver (Australis 26 k, Lawnton, Australia). Radio-tagged birds were first located from a distance from the radio signal and, once visual contact was made with the foraging bird, the exact site of a successful prey capture was identified with the aid of binoculars and marked with a labelled stick. Then, a control plot was generated by selecting a random angle (0–359°) and a random distance (between 26 and 100 m) from the actual foraging plot.

In Italy, breeding individuals were visually tracked when flying from the nest to foraging sites, with the aid of binoculars (Brambilla et al., 2017b). Once a foraging event was encountered, the exact location was recorded with a GPS device or by mapping the point on a detailed aerial photograph. The foraging location was established as the first position where a food item was collected (or as the last location of the bird before returning to the nest, when we could not directly assess prey capture, since snowfinches usually provision food to the nest

immediately after prey capture; Brambilla et al., 2017a). After the collection of 10 foraging locations per study pair, an equal number of control plots (with the only constraint that they should not overlap with foraging plots) were randomly selected within a radius of 300 m around the nest (Brambilla et al., 2017b; Grangé, 2008; Strinella et al., 2007) so as to map habitat characteristics.

The difference in the methods used for the selection of control plots between Switzerland and Italy did not affect the results, as control plots showed similar suitability values across the two approaches (as revealed by a mixed model analysing habitat suitability of control plots including site identity as a random factor and methods of control plot selection as fixed effect, where the AIC value was larger than the null model; Table A3).

Habitat cover and structure were recorded within a 5 m-radius around each foraging location and control plot. Habitat variables described vegetation and other ground cover, as well as sward height and the occurrence of grazing (Table 1). In addition, topographical features (slope, solar radiation) were calculated in a geographic information system (GRASS 7.04) using detailed Digital Elevation Models (resolution between 1 and 5 m) made publicly available by regional/provincial authorities in Italy and by SwissTopo maps for 2013 (Swiss Federal Office of Topography). Solar radiation was calculated as global radiation on 21st June, taking into account the shadowing effect of the relief.

Sward height could not be recorded where grass was absent ($n = 16$ locations out of a total of 470). Because of this, in exploratory analyses we compared the modelled relationships between foraging occurrence and sward height by setting sward height to zero at these 16 locations or by omitting these locations from the analysis. Given that the coefficients for sward height were very similar between models with or without 'filled gaps' (−1.02 and −1.03, respectively), we decided to apply the former option.

2.2. Statistical analyses

2.2.1. Foraging habitat selection

Habitat variables were recorded at 470 locations (235 foraging and 235 control plots) obtained from 22 breeding pairs (see Table A1 for summary statistics). All variables were standardized (i.e. centred on their mean value and scaled by their standard deviation) before analyses. After checking for outliers and zero-inflated variables, sand and mud cover were discarded, and human-altered habitats (two types of roads and urbanized areas) were joined into a single variable (anthropized areas).

We modelled foraging habitat selection by means of conditional logistic regression (Hosmer and Lemeshow, 1989), which accounts for the intrinsically paired nature of the sampling protocol and resulting dataset. According to this approach, each set of foraging plots of a given breeding pair was matched to the respective control plots, henceforth taking into account the pair-based sampling design. Pair identity was thus specified as a so-called "stratum" variable. Conditional logistic regressions were run by using the 'clogit' function of the 'survival' package in R (R Development Core Team, 2016).

Model selection was performed using an information-theoretic approach, based on the Akaike's Information Criterion adjusted for small sample sizes (AICc) (Burnham and Anderson, 2002). First, to reduce the risk of model overfitting and to limit the potential effects of multicollinearity, the explanatory variables were divided in two groups (Assandri et al., 2018). These groups were "vegetation" and "other variables" (Table 1). We tested for within-group collinearity by calculating the variance inflation factor (VIF) using the package *car* in R (R Development Core Team, 2016). For all variables within a given group, there were no collinearity issues ($VIF < 3$ for all variables in both groups). Within each group, models with all possible variable combinations were constructed, and models were ranked according to their AICc value using the MuMIn package (Bartoń, 2016). The difference in AICc between each model and the top-ranking model ($\Delta AICc$) was

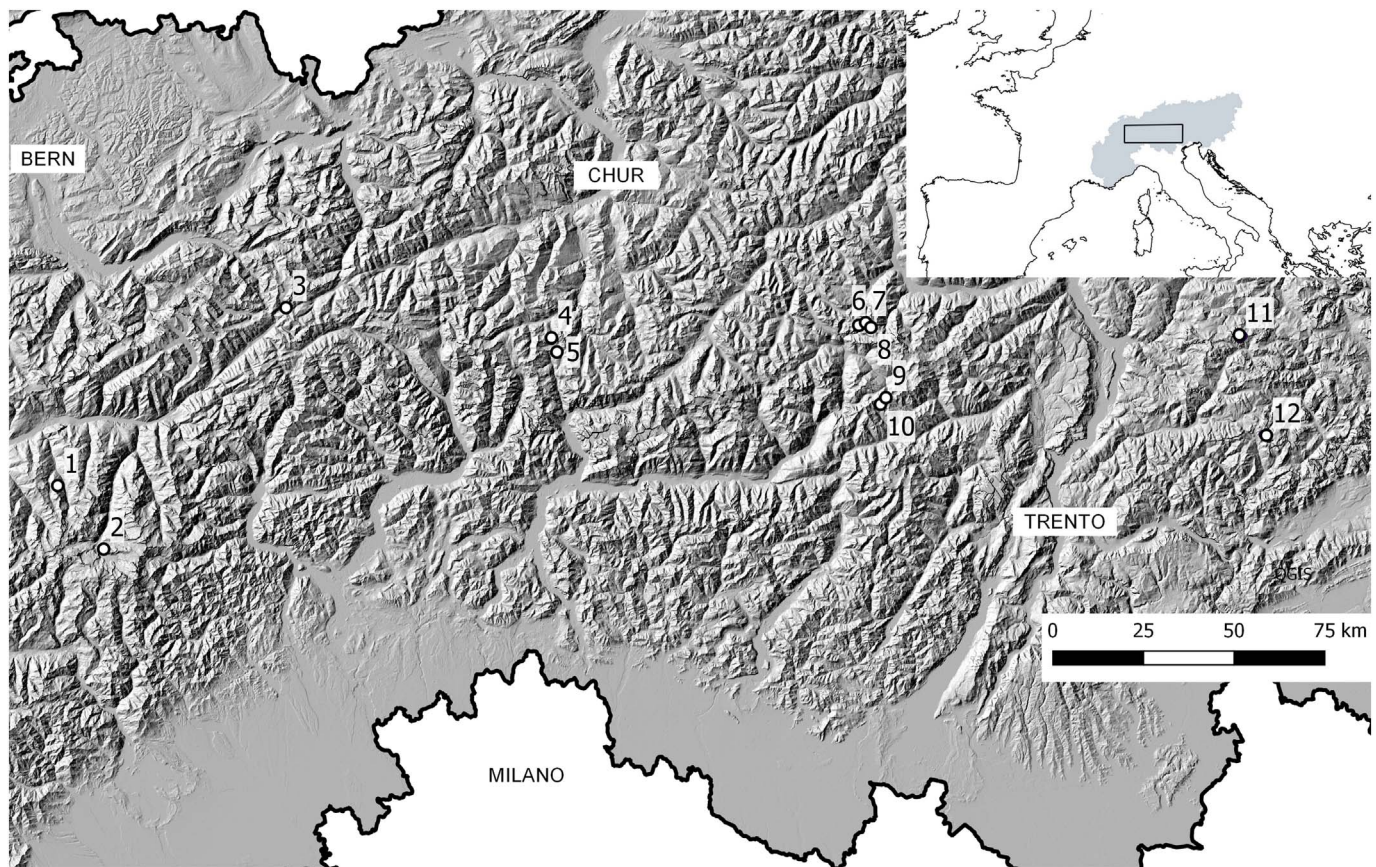


Fig. 1. Map of the study area showing the 12 study sites monitored in the Swiss and Italian Alps (1: Sorebois; 2: Zermatt; 3: Furka Pass; 4: Passo Spluga; 5: Montespluga; 6: Valle del Braulio; 7: Passo Umbrail; 8: Passo dello Stelvio; 9: Rifugio Gavia; 10: Passo Gavia; 11: Passo Sella; 12: Rosetta). The location of some major towns (Bern, Chur, Milano and Trento) is also given for a better interpretation of the geographical extent of the study area. The inset shows the location of the study area (rectangle) within the European Alps (grey).

calculated. Based on a previous study, we hypothesised that snowfinches would preferentially forage in sites with high grass cover but low sward height (Brambilla et al., 2017b). Therefore, we added a potential interaction term to the “vegetation” group (grassland cover $\times$ sward height). Moreover, in order to test for selection of melting snow patch margins (see e.g. Antor, 1995) and according to preliminary data exploration (which suggested a potential curvilinear relationship for snow cover), we also included a quadratic term for snow cover (in the “other variables” group). Then, for each group we selected all the variables (and interactions) included in the most supported models ($\Delta\text{AICc} < 2$) after the exclusion of ‘uninformative parameters’ (i.e. variables for which inclusion resulted in a higher AICc value of the model, but with an increase in AICc < 2 ; Arnold, 2010; Jedlikowski et al., 2016). We finally combined the retained variables of both groups and carried out a further model selection using the same procedure (see e.g. Assandri et al., 2016; Brambilla et al., 2017c). In the latter process, given that snowfinches could preferentially forage in fine-scaled mosaics of snow and grass (Brambilla et al., 2017b), we added the interaction term snow $\times$ grassland cover.

2.2.2. Past, current and future habitat suitability

To predict climate-driven changes in foraging habitat suitability, we modelled snow cover and sward height as a function of season progression and environmental characteristics, selected on the basis of a potential effect of climate on those two variables according to the literature and expert opinion. We built models based on the control plots, which were randomly selected and thus ensured unbiased sampling (snowfinches may select patches where micro-topography or other local conditions can result in values of snow cover or sward height deviating from the average values of each territory). First, we built a model

relating snow cover to Julian date, solar radiation, elevation and slope. Then, we modelled sward height as a function of solar radiation, elevation, slope, snow cover and grazing occurrence, excluding the few sites without grass cover. In both cases, we used linear mixed models (LMM) considering breeding pair as a random factor to take into account the spatial dependency of control plots within areas frequented by the same breeding pair. Effect size for variables in the mixed models was calculated according to the semi-partial R^2 statistic proposed by Jaeger et al. (2017) using the *r2glmm* package in R.

We estimated past and simulated future conditions based on the observed rate of change in the date of snow melt: research from the Swiss Alps reported a linear pattern of advance in snow melt timing by c. 6 days per decade (5.8 days/decade; Klein et al., 2016). To hindcast past conditions (40 years ago), we therefore decreased the sampling date by 24 days. To model conditions 50 years into the future (at year 2066), we added 30 days, assuming the trend in melting pattern will remain unaltered. We then recalculated predicted snow cover and grassland height for each of the three time steps (in the following termed ‘past’, ‘current’ and ‘future’).

Finally, we calculated for each plot (foraging or control, $n = 470$) the potential suitability under past, current and future conditions, by means of the final habitat selection model obtained in the previous analysis, and averaged predicted habitat suitability for all plots related to each breeding pair. We used modelled snow cover and sward height (i.e. predicted values from snow cover and sward height models), instead of the values actually recorded in the field, including model predictions for the current period in order to eliminate the effect of the site- and time- specific conditions associated with the sampling period and to obtain habitat suitability estimates that were comparable with past and future conditions. In this estimation of habitat suitability in

Table 1

List of habitat variables measured within a 5-m radius at foraging and control plots, with information about methods, metrics and descriptor category. Ground cover variables sum up to 100%. For the statistical analyses, sward height, grassland cover, shrubs cover were assigned to the “vegetation” group, whereas all the others were assigned to the “other variables” group.

Variable type/ variable name	Description	Unit
Vegetation structure		
Sward height	5 measurements of grass height at the plot centre and at 2.5 m along each of the four cardinal directions (or at the closest point with grassland cover, respectively)	cm
Ground cover		
Grassland	Cover of grassy vegetation	%
Shrubs	Dwarf-woody vegetation (e.g. <i>Rhododendron</i> , <i>Juniperus</i> , <i>Salix</i> ...)	%
Snow	Snow-covered areas	%
Boulders	Rocks detached from the substrate	%
Bare ground	Bare soil (compact soil)	%
Rocks	Emerging rocky substrate (bedrock)	%
Scree	Small rocky material (a few cm in diameter)	%
Gravel roads	Unpaved roads, large footpaths	%
Paved roads	Roads, paved parking	%
Sand	Sandy soil (not compact)	%
Urbanized	Buildings, walls, pylons	%
Water	Lakes, ponds, watercourses	%
Other	Other uncovered categories	%
Grazing occurrence	Dung of current or previous year or active grazing	Yes/no
Topography		
Slope	Angle in degrees (°) calculated at the plot center using a digital elevation model (resolution: 1–5 m)	Degree
Solar radiation	Calculated as global radiation for 21st June based on a digital elevation model, incorporating the shadowing effect of the surrounding relief	kWh/m ²

different periods, we used the original values for the two other variables (cover of grassland and of anthropized areas) included in the habitat selection model.

2.2.3. Mitigation scenarios

To simulate and evaluate any potential benefits of targeted management actions to maintain foraging microhabitat suitability, we also modelled current and future suitability under two scenarios, with and without mitigation management. The ‘non-mitigation’ scenarios (without management) corresponded to the modelled habitat suitability as described above. For the mitigation scenarios (via habitat management), we assumed that sward height would be managed according to optimal snowfinch requirements by keeping grass height below 6 cm (see Fig. 2 and Brambilla et al., 2017b). We assumed that such optimal sward height could be achieved by mowing or controlled grazing. We therefore used the predicted sward height under current and future climate conditions, respectively, both adjusted by truncating the highest values at 6 cm. Finally, to evaluate whether habitat suitability significantly changed from past to current and from current to future conditions under both scenarios (with vs without management), we performed a Wilcoxon matched-pairs test on the mean plot suitability for each pair. For descriptive purposes, we also counted the number of plots with average plot suitability above 0.5 (suitable plots) for each time step (past, current, and future).

3. Results

3.1. Foraging habitat selection

We obtained a single most supported synthetic model, as all other

candidate models (after the exclusion of uninformative parameters) had a $\Delta AICc > 2$ (Table A2). According to this model ($R^2 = 0.35$), the most suitable foraging habitats were characterized by low sward height and cover of anthropized areas, intermediate snow cover and high grassland cover (Table 2). Effect sizes for these variables ranged between 0.17 and 0.34, with snow cover and sward height having the largest effects (Table 2). The influence of these predictors on the probability of occurrence of foraging snowfinches is shown graphically in Fig. 2.

3.2. Past, current and future habitat suitability

The model for snow cover (intercept: -0.19 ± 0.10) suggested, as expected, a positive effect of elevation (0.24 ± 0.11 , effect size: $r = 0.28$) and negative effects of Julian date (-0.13 ± 0.07 , $r = 0.17$), slope (-0.05 ± 0.09 , $r = 0.04$) and solar radiation (-0.08 ± 0.09 , $r = 0.07$), and had a conditional R^2 equal to 0.23. The model for sward height revealed a positive effect of solar radiation (0.26 ± 0.09 , $r = 0.23$) and slope (0.47 ± 0.09 , $r = 0.41$): well exposed steep slopes are likely those where snow disappears earlier and where the plant growing season may start earlier, leading to higher swards. As expected, a negative effect on sward height was found for grazing (grazing occurrence: -0.08 ± 0.15 , $r = 0.05$), elevation (-0.60 ± 0.14 , $r = 0.61$) and snow cover (-0.14 ± 0.08 , $r = 0.15$), likely due to both different grass species at different elevations and to the delay in growing season caused by elevation and snow cover. The model for sward height had a conditional R^2 equal to 0.53.

Foraging habitat suitability was predicted to have declined from 1976 to 2016, and to continue declining from 2016 to 2066 at all breeding sites (Fig. 3). The predicted average site-level plot suitability had strongly declined from 1976 to 2016 (Wilcoxon matched pairs test, $Z = -4.11$, effect size: $r = 0.71$, $n = 22$ breeding sites), and is expected to greatly decline further by 2066 ($Z = -4.11$, $r = 0.71$). The overall number of suitable plots (plots with habitat suitability higher than 0.5; $n = 470$) declined from 364 (77%) to 281 (60%) from 1976 to 2016 (–23% in the number of suitable plots), and was predicted to further decline to 191 (41%) by 2066 (i.e. a further change of –32% in the number of suitable plots relative to the current situation).

3.3. Mitigation scenarios

The mitigation scenarios yielded higher current and future habitat suitability values than the estimates obtained without any intervention targeted at limiting sward height, especially for sites with most or some plots located at the lower end of the elevational range exploited by the species (Fig. 3). Under current conditions, if appropriate management actions were implemented, the number of suitable plots would be 359 (76%; which roughly corresponds to the figure back-projected to 1976 without management), while the average territory-level plot suitability would be significantly higher ($+0.07$; Wilcoxon matched pairs test; $Z = -3.52$, effect size: $r = 0.62$, $n = 22$ breeding sites) compared to a scenario without management. The future number of suitable plots under an active mitigation scenario would be 268 (57%; very close to the number of currently suitable plots). Compared to a scenario with no management implemented in the future, average habitat suitability could thus be increased by 0.07 (Wilcoxon matched pairs test; $Z = -3.52$, $r = 0.62$, $n = 22$ breeding sites) via mitigation measures.

4. Discussion

Our retrospective and prospective modelling showed that a climate-sensitive species of high-alpine ecosystems, the white-winged snowfinch, is at risk from microhabitat loss induced by climate warming, confirming at a fine-scale level previous suggestions derived by large-scale modelling (Brambilla et al., 2016, 2017a). Not only has it seemingly already lost a substantial fraction (–17% of plots, or –23% of suitable plots, from 1976) of its structurally suitable foraging habitat in

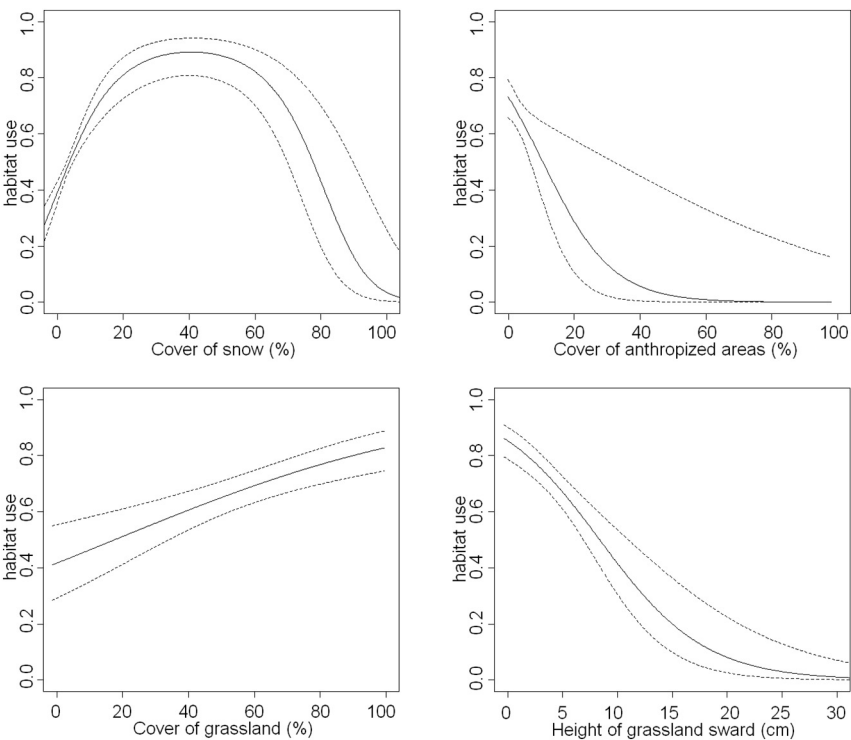


Fig. 2. Effects of habitat variables affecting the probability that a bird foraged in a given habitat patch according to the best-fitting conditional logistic regression model reported in Table 2. In each panel, the variable's effect on predicted probability of habitat use (mean and 95% confidence interval) are shown while all other predictors included in the models are kept at their mean value.

Table 2
Best-fitting conditional logistic regression model for foraging habitat selection by breeding snowfinches during the nestling rearing period. Effect size (Pearson's *r*) was computed considering a sample size equal to 235 dyads.

Variable	Estimate (SE)	Z	P	r
Grassland cover	0.57 (0.14)	4.14	< 0.001	0.26
Sward height	−0.85 (0.16)	5.37	< 0.001	0.34
Snow cover	2.00 (0.32)	6.18	< 0.001	–
Snow cover ²	−0.72 (0.13)	5.32	0.003	0.34
Anthropized	−1.21 (0.45)	2.65	0.008	0.17

the Central European Alps over the past decades, but the unabated habitat alterations induced by climate change would also continue to reduce habitat suitability in the decades to come (−19%, or −32% of suitable plots, by 2066). To the best of our knowledge, this is the first study that has quantified fine-grained microhabitat requirements for reconstructing past, and predicting future, foraging habitat suitability in a high-elevation species, i.e. a species occurring in an ecosystem that is more affected by climate change than the global average (see Moritz and Agudo, 2013 and references therein). Indeed, most research on the impact of climate change on biodiversity has so far dealt with modelling macro-ecological relationships between climate and species' biological attributes (Bellard et al., 2012). Even if such broad-scale correlative models could identify the pool of species in a given area that are likely to be mostly impacted by climate change, more detailed approaches (like the one we have adopted here) are required to produce accurate projections of changes in fine-scale habitat suitability and to assess the potential effectiveness of habitat management as a mitigation measure. This study is also one of the first to illustrate that mitigation measures (targeted sward management by grazing) could be implemented to maintain habitat suitability and thus buffer against the detrimental effects of climate change, in line with what Braunisch et al. (2014) have proposed for montane and subalpine forest bird species, and with what Regos et al. (2017) suggested for birds in wildfire-prone ecosystems. This lack of fine-grained mechanistic studies of habitat selection is surprising as understanding species' ecological requirements is a prerequisite both for sound modelling of species-habitat relationships and

for designing adequate mitigation strategies for conservation. In particular, microhabitat selection studies carried out during the main bottlenecks of a species' life cycle, notably the critical and intense phase of food provisioning to offspring (nestlings), are key as breeding output depends on parental investment into progeny. The mechanical links evidenced in our field surveys between environmental characteristics favouring foraging activity (snow cover and sward height) and the alterations of these characteristics induced by climate warming exemplify how meaningful forecasting of future species distributions via spatial modelling should operate to gain predictive power. The general lack of fine-grained studies is probably linked to the intensive and time-consuming data collection required, and such studies are unlikely to be feasible for a large number of species at the same time. Additionally, the high-precision information required for the study we carried out prevented similar modelling over broad scales (e.g. at the regional or continental level), even if the increasing availability of high-resolution data will likely allow new steps in that direction in the near future.

4.1. Microhabitat suitability for foraging snowfinches is affected by climate-related habitat variables and anthropization

Breeding snowfinches collected food for nestlings in microhabitats characterized by intermediate snow cover intermixed with short grassland, while avoiding human-altered areas, notably roads and buildings. These results are in line with previous findings obtained at a much coarser scale in a largely overlapping study area, where snowfinches were also found to primarily select short grassland and snow-covered areas (Brambilla et al., 2017b). In addition, at a coarser scale, snowfinches were found to be associated with sites with lower solar radiation (especially later in the season, when those sites are the ones most likely to be still covered by snow and with short vegetation), bare ground and some boulders (Brambilla et al., 2017b), which were no longer important at the fine scale we considered. The preference for an intermediate snow cover (optimum at c. 40%) reflects the species' foraging tactics: snowfinches either collect invertebrate fallout on the snow surface (Antor, 1995), or exploit the melting margins of snow fields where they can find abundant tipulid larvae, one of their

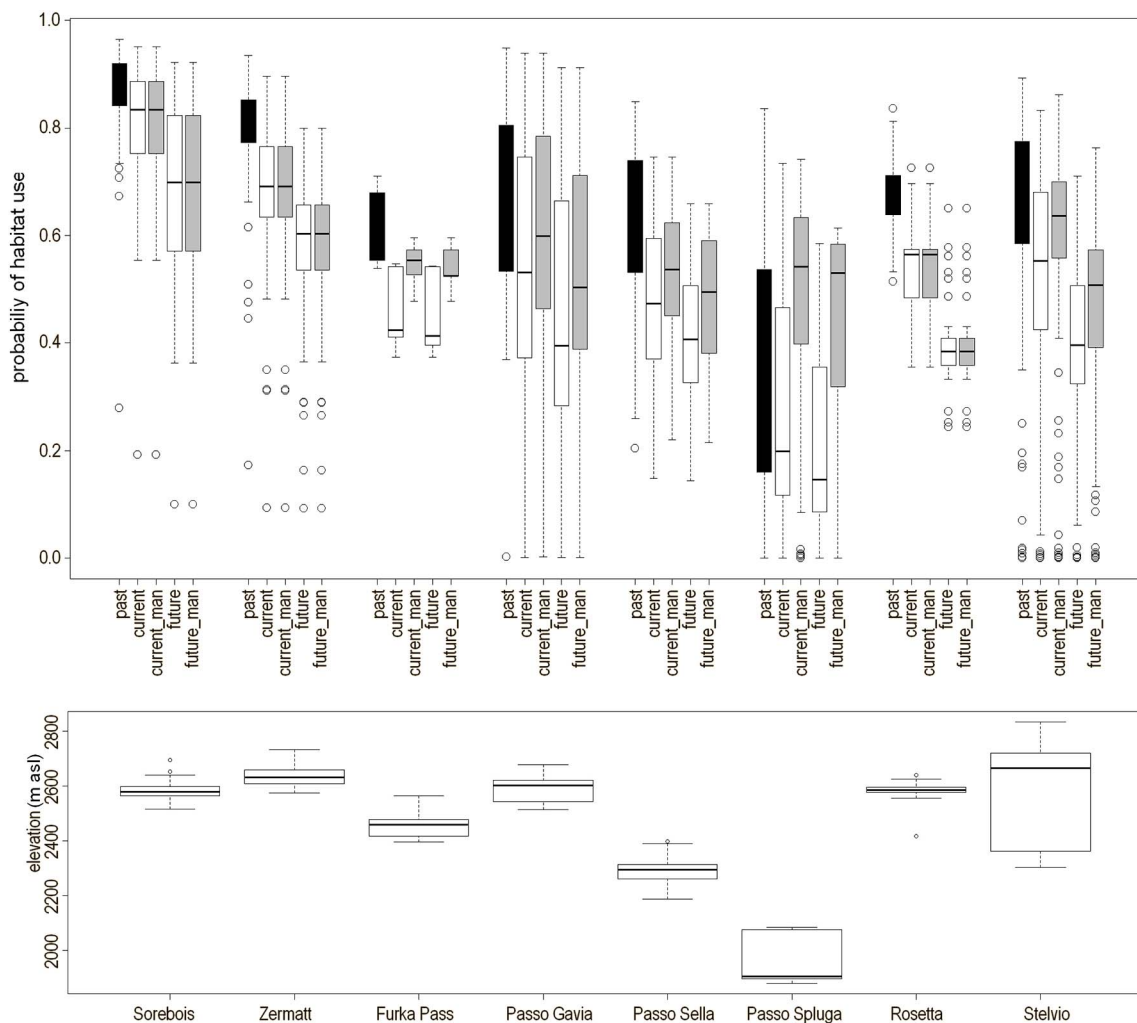


Fig. 3. Upper half: boxplots of past, current and future habitat suitability of all sampled plots ($n = 470$) within each study site ($n = 8$ sites), according to the best-fitting model of microhabitat selection and the simulated scenarios of managed vs. unmanaged grassland sward height (in the managed scenario, grassland sward was kept at a maximum height of 6 cm; see [Methods](#) section for details of the procedure). For each site, boxes show from left to right habitat suitability for different time steps and scenarios: past (black), current – unmanaged (white), current – management scenario (grey), future – unmanaged (white), future – management (grey). Plots show median, upper quartile, lower quartile, maximum and minimum values excluding outliers, i.e. value above 1.5 the upper quartile or below 1.5 the lower quartile. Lower half: boxplot of plot (foraging and control) elevation within each study site.

favourite and most profitable prey items ([Cramp and Perrins, 1994](#)). Sward height constrains foraging opportunities: short grass is likely to boost prey availability, which is prey abundance modified by its accessibility ([Schaub et al., 2010](#)). Yet, to further refine our mechanistic understanding of microhabitat associations, future work should also investigate how prey abundance varies with respect to snow cover and the melting front of the snow field in particular, and throughout the breeding season in relation to the different habitat types in general.

Overall, our findings confirm that properly predicting mountain birds' responses to global change necessitates the consideration of both climate and habitat factors simultaneously ([Chamberlain et al., 2016a](#)), as habitat traits could be extremely important and interact with climate change itself ([Sirami et al., 2017](#); [Titeux et al., 2017, 2016](#)). High-elevation species spend a large part of their life-cycle in extreme habitats. They have thus evolved specific adaptations to cope with harsh environmental conditions ([Cheviron and Brumfield, 2012](#); [Gobbi et al., 2017](#); [Scridel et al., 2018](#)). However, climate change is accompanied by increased weather variability and an acceleration of extreme events, which represents a new evolutionary challenge for biodiversity in general ([Di Marco and Santini, 2015](#)) and high-alpine biodiversity in particular ([Lu et al., 2009](#)). The effects of the increased weather variability and frequency of extreme events on the suitability of foraging habitats also deserve further investigation. Moreover, direct

anthropogenic impacts on Alpine ecosystems are increasing: the tourism industry modifies high-elevation landscapes and biodiversity via the creation of new infrastructures (e.g. [Rolando et al., 2007](#)), recreational disturbance (e.g. [Arlettaz et al., 2015, 2013, 2007](#)) and other anthropogenic stressors ([Chamberlain et al., 2016b](#); [Scridel et al., 2018](#)). Although the snowfinch is considered a synanthropic species benefiting from human infrastructures both for nesting (mountain buildings, ski-lift pylons and even nest-boxes) and winter foraging (seed-feeding stations at ski resorts or mountain chalets) ([Cramp and Perrins, 1994](#)), our results show that roads, paths, buildings and other man-made structures decrease foraging microhabitat quality during the reproductive period. It would thus be particularly interesting to estimate the year-round costs and benefits of breeding in anthropized in contrast to natural habitats.

Climate change can threaten alpine species to such an extent that the large-scale distribution of species like the snowfinch could shrink considerably ([Brambilla et al., 2017a](#); [Maggini et al., 2014](#)). Our study demonstrates a high sensitivity of snowfinch towards climate-induced alteration of microhabitat conditions, notably in snow cover and sward, shedding light on the possible mechanistic causes behind the ongoing range contraction of this and other cold-adapted species ([Scridel et al., 2017](#)). Warming climate induces both an anticipation of the seasonal timing of snowmelt ([Klein et al., 2016](#)) and an earlier and faster grass

growth at high elevations (Theurillat and Guisan, 2001), which affects the snowfinch as well as other elements of alpine biocenoses (Pettorelli et al., 2007).

A note of caution should be made about our models for snow cover and sward height. On the one hand, the snow cover model had a rather low explanatory power, suggesting that local conditions may be very important in driving seasonal patterns of snow cover changes. In particular, winter precipitation and spring temperature are crucial in determining how long snowfields can last during the snowfinch breeding season. Therefore, improving the modelling of snow melting patterns at a high spatial resolution would be an important future task for a better assessment of changes in foraging habitat suitability for alpine birds. On the other hand, sward height may also depend on the pool of locally occurring grassland species. Despite this, the sward height model performed very well, suggesting that common patterns in the study area can be detected even without considering grassland species' composition. Hence, our results can be considered as representative of the general patterns of snow cover and sward height variation experienced by snowfinches in the Alps.

4.2. Buffering climate change impacts via habitat management

While slowing down climate warming requires long-term global measures to drastically reduce society's reliance on fossil energy sources, sward management through targeted grazing is amenable to local action. Our model outcomes suggest that the management of sward height might offer some room to buffer the negative impacts of climate warming on foraging microhabitat configuration, especially for sites located at relatively low elevation, where grassland cover and sward height play a crucial role in determining habitat suitability for snowfinches (for sites located at higher elevation or with low grassland cover, this would hardly provide any tangible benefit – see e.g. the first plots on the left side of Fig. 3). According to our proposed scenario, a systematic implementation of sward height management at our study sites would have compensated for the decline in structural microhabitat suitability that has occurred from the 1970s and could also strongly reduce the predicted reduction of foraging habitat suitability over the next 50 years. However, it remains to be seen whether: 1) other effects of climate change may turn into unsuitable also the sites where foraging habitat can be kept structurally suitable by means of management, and 2) implementing this measure would be sufficient to compensate for the effect of the snowpack reduction and earlier snowmelt, which may directly or indirectly impact on the invertebrate community upon which alpine birds feed. If the dependence on accessible foraging grounds is the main factor, then management might effectively increase habitat suitability. However, if the conditions prevailing along the melting snow front dictate not only prey accessibility, but also prey abundance and phenology, this measure will likely not suffice, unless the snowfinches can alter their breeding phenology towards earlier nesting. This emphasizes the need to better understand, first, how invertebrate prey availability (which is, again, abundance modified by accessibility) drives foraging microhabitat selection (Vickery and Arlettaz, 2012); and, second, what is the adaptive potential of the species to environmental change, notably in terms of plasticity in reproductive phenology. From this point of view, the results of our retrospective habitat suitability model suggest that the snowfinch might have a limited capacity to cope with environmental change, notably with the ongoing major alterations in snow cover conditions. Investigations of its long-term breeding phenology are also needed to further appraise its adaptive potential. Finally, preventing the construction of new infrastructures at high elevation, converting disused tracks at construction sites into grassland, as well as ski-piste revegetation (Caprio et al., 2016), may limit or reduce further losses of suitable habitats due to human activities.

Future studies should evaluate whether a generalization of our recommendations is possible, both from a spatial and a taxonomic point

of view. Indeed, keeping a low sward height could also favour prey capture by breeding snowfinches in the other parts of the species' breeding range. Similarly, this management regime could favour other insectivorous birds requiring low swards (Vickery and Arlettaz, 2012) that dwell in alpine grassland, such as water pipit *Anthus spinoletta*, ring ouzel *Turdus torquatus*, alpine accentor *Prunella collaris* or northern wheatear *Oenanthe oenanthe*. More generally, the potential consequences of grassland management on plant species (for which grazing or mowing could be both beneficial or counter-indicated, Pierce et al., 2007) and habitats should also be evaluated locally.

The present study highlights the importance of considering microhabitat selection for revealing fine-scale, functional and interacting effects of climate and land-use changes on climate-sensitive species and for identifying compensatory habitat management strategies that could to some extent allow buffering the negative effects of climate warming on high-elevation biodiversity.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2018.03.008>.

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